MATING BEHAVIOR OF A NEW GUINEA *LUCIOLA* FIREFLY: A NEW COMMUNICATIVE PROTOCOL (COLEOPTERA: LAMPYRIDAE)[1]

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ABSTRACT

Luciola obsoleta (Olivier) has the most complex mating behavior reported for Lampyridae. It mates in sedentary groups (aggregations?): the basic stages of its mating protocol seem to be (1) sedentary signalling, (2) chasing, (3) walking-luminescing, (4) mounting, and (5) copulating. This behavior suggests that this *L. obsoleta* may be but one of a complex of cryptic species.

Fireflies of many species use luminescent mating signals. Two basic signal systems or behavioral protocols are used in conjunction with light emission (Lloyd, 1971): in *Lampyris noctiluca* L. stationary females glow continuously and flying males approach the glows (System I); in *Photinus* spp. males flash a brief and characteristic pattern and females respond after a species-typical time interval. The males then fly and walk to the females, and during this approach they maintain a flash dialogue (System II). The protocol of the New Guinea firefly, *Luciola obsoleta* (Olivier), differs from both of these systems and is more complex, since it involves not only coded luminescent emissions, but also spatial movements, and perhaps their interplay.

I observed *L. obsoleta* in a small cocoa grove within a second-growth, sea level rain forest near Alexishafen, New Guinea, in September and October, 1969. The first flashes each evening were emitted 8-21 min. after sunset ($\overline{x} = 15$, $n = 6$), and flashing activity was intermittent from then until dawn. Males flashing during the first few minutes of activity were commonly (in samples on successive nights, 4 of 6 and 4 of 7) those that were just separating from females with which they had coupled the previous night, such pairs having remained motionless in vegetation throughout the day.

SEDENTARY SIGNALLING

The most conspicuous aspect of the behavior of this firefly was its sedentariness—only occasionally did one or a few fly during light emission. Luminescing individuals were usually perched in weeds and the lower branches of cocoa trees, in one or a few scattered and loose aggregations. One aggregation that I studied extensively was approximately 50 ft. in diameter and numbered 50-100 individuals. Most flashing males were standing near, or walking along, the edges of leaves, and had their

[1]This investigation was conducted during Program C, 1969 Helix Expedition to New Guinea, supported by grant GB8400 for the National Science Foundation to the University of California, Scripps Institution of Oceanography. Vouchered specimens have been deposited in: Florida State Collection of Arthropods; U.S. National Museum, and Cornell University.

heads extended well out from under their pronota and over the leaf edges. In one sample of 20 flashing males, 13 were standing at leaf edges with head extended, 5 were walking along a leaf edge, and 2 were walking, but not at an edge.

The most common luminescent emissions of males were flickers and single flashes, but even to the unaided eye this dichotomy was not distinct. Modulations were often discernible in single flashes, and flickers were often short and erratic (twinkles). Electronic analysis confirmed these visual impressions and revealed other subtleties (Fig. 1-7). Flickers were frequently of short duration (i.e., less than 5 sec) but some lasted 20-30 sec. Frequency of modulations during flickers varied from 3-10 Hz (Hertz)[2] and seldom remained constant for more than 3 sec in a given flicker (Fig. 5). For example, in successive one-sec periods in one recorded flicker, frequencies were 4.1, 4.5, 4.7, 5.3, 6.5, 7.3, 6.3, 6.2, 6.3, 6.0, 6.4, 6.6, 6.1, 5.0, 4.5, 3.2; and in another 7.2, 6.6, 7.5, 7.8, 6.6, 6.2, 5.6, 7.5, 6.5, 7.3, 7.0, 7.3, 7.4, 6.9, 7.0, 5.2, 4.3, 6.8, 7.7, 8.5. Males that were emitting single flashes began flickering when I gently touched the leaf upon which they were standing (Fig. 6); the frequencies of these were 7-9 Hz at first, then dropped to 4-5 in 2 or 3 seconds, and in a few seconds ended with the resumption of single flashes.

Single flashes were frequently bimodal or trimodal. The relative intensity and time separation of the modes varied, and the visual impression of some was that their intensity increased in a stepwise manner (Fig. 4). The duration of single, simple flashes was 0.06-0.13 sec ($\bar{x} = 0.10$, $n = 116$, 17 males) (Fig. 2). The duration of bimodal and trimodal flashes was variable (Fig. 7) (such flashes may represent independent, non-synchronous, single flashes of the 2 segments of the light organ). Flash periods or intervals were also variable. For example, consecutive periods (mixture of simple and compound flashes) of 2 perched males were 0.34, 0.34, 0.34, 0.43, 0.60, 0.64, 0.48, 0.60, 0.60, 0.64, 0.62, 0.56, 0.42, 0.58, 0.42, 0.30, 0.18, 0.19, 0.17, 0.43, 0.48; and 0.43, 0.60, 0.16, 0.32, 0.62, 0.73, 3.34, 0.56, 0.40, 0.52 sec.

The luminescent emissions of females appeared to be modulated and unmodulated glows of various intensities. The conspicuously modulated glows (beady glows) sometimes had minor intensity variations superimposed upon the major modulations (Fig. 8 & 9). Glows, that appeared in the field to be unmodulated, sometimes had flickers up to 8 Hz (Fig. 10), and at other times were without modulations (Fig. 11). One female superimposed bright flashes upon a continuous, steady glow (Fig. 12). Both sexes alternated, with no discernible schedule or routine, their 2 basic emission patterns; infrequently 1 emitted a pattern more typical of the other. Unless otherwise noted or illustrated, the descriptions of luminescent signals below are based upon visual observations and impressions, and not electronic recordings.

There was no discernible interplay of signals between sexes as found in American species using signal system II. Occasionally indiyiduals flew a few feet or yards; flying males emitted flickers with frequencies similar to those of perched males, and flying females emitted modulated or unmodulated glows.

[2]Hertz=cycles per second; all recordings made at 25.5°C. (78°F).

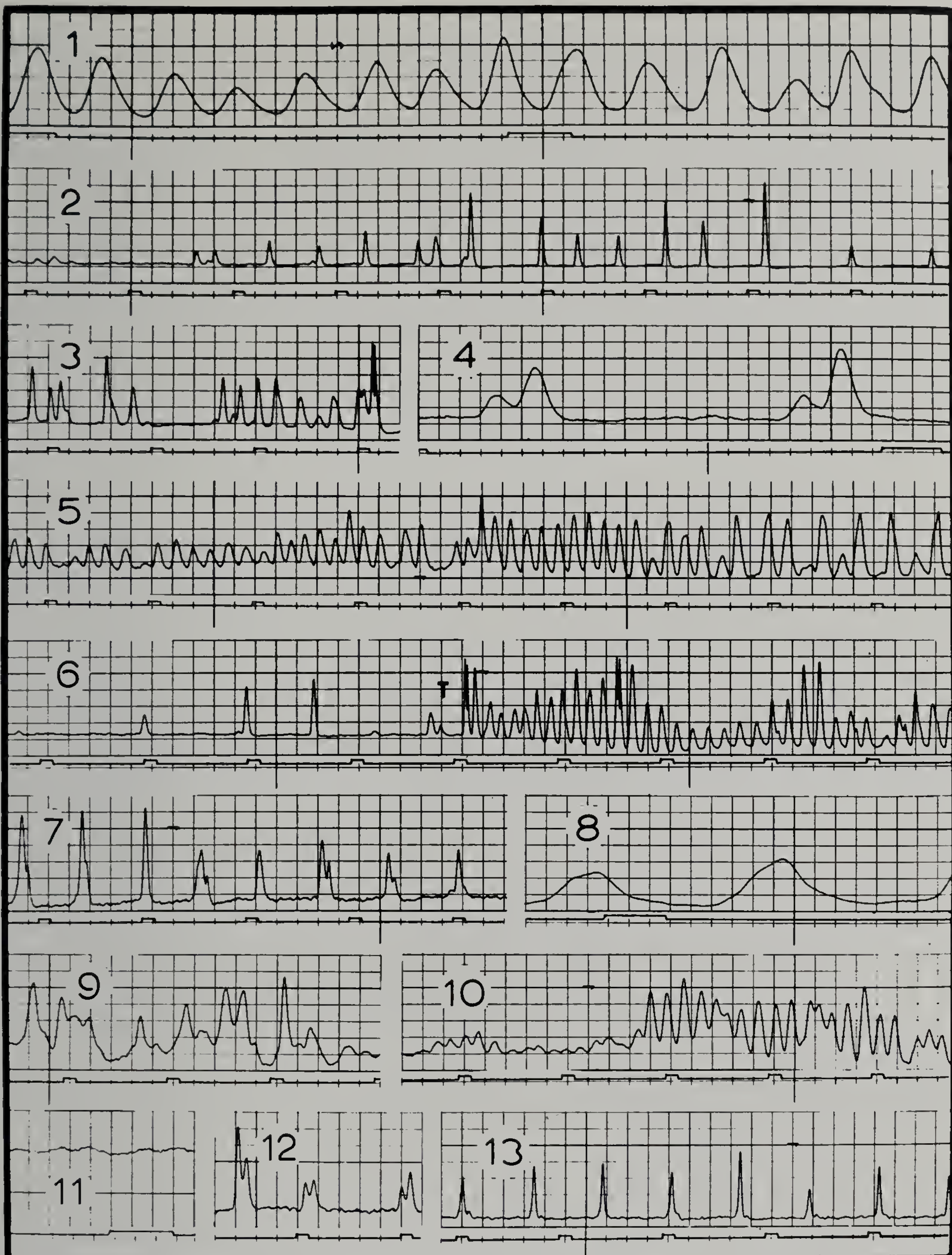

Fig. 1-13: luminescent emissions of *L. obsoleta.* Charts (Brush Mark 220) read left to right. Vertical axis, relative intensity; horizontal axis, time, scale as indicated by 1-sec (period) marker below firefly trace (marker duration 0.12 sec). Recording temperature 25.5°C. 1) Flicker of perched male. 2) Simple and compound single flashes of perched male. 3) Short erratic flickers of perched male (twinkles). 4) Stepped flashes of perched male. 5) Flicker of perched male; note frequency changes and compound modulations. 6) Single flashes, then flicker of perched male; (T) marks moment perch of male was gently touched. Distortions (heavy marks) at peaks of 2 modulations due to very bright modulation overloading recording equipment. 7) Single flashes of perched male; note varying time relationship of flash peaks within compound flashes. 8) Beady glow of perched female. 9) Beady glow with superimposed modulations, of a perched female. 10) Modulated glow of landing female: appeared to be steady glow. 11) Steady glow of perched female. 12) Female flashes superimposed upon glow. 13) CFP (characteristic flash pattern) of male mounted upon female; note period regularity, and changing position of minor peak with respect to major peak.

Many different kinds of interactions occurred between individuals. Both males and females commonly landed a few inches or feet from perched, luminescing ones. Perched males would sometimes begin flashing as a male or female flew over them. Males sometimes hovered and flickered a few inches above perched individuals, darting toward and away from them, and they sometimes landed next to them. Males also flickered and flitted about glowing cigarettes, dim lights on recording equipment, and hand-held vials containing glowing females. They occasionally hovered in front of my unlighted head lamp, perhaps responding to the reflection of their own luminescence.

Chases

The most conspicuous interactions between individuals were chases of flying, glowing females by flickering males. Usually 1 or 2 males pursued a single female, but chases involving up to 4 males were observed (in 40 naturally occurring chases, 20 involved 1 male, 14 involved 2 males, 4 involved 3 males, 2 involved 4 males). Males joined chases or pursued lone females from as far away as 15 feet and sometimes pursued them 100 ft or more. Glowing females in hand-held vials, and a small penlight, when moved through the air near males, would sometimes elicit pursuit. Chases were observed only after 144-164 min past sunset; before this time, flying females did not elicit male pursuit. This time threshold, first noted through observation of natural chases, was confirmed experimentally by releasing females within a few feet of perched, flashing males.

Chases usually ended within 30 feet of where they started, with the female and 1 male perched within a few inches, usually 4 or less, of each other on a leaf. During a chase males sometimes darted sharply toward and appeared to bump the females, frequently causing the females to drop abruptly and land.

Males were more successful in pursuing and landing with females if no other males participated: in 20 of 27 chases involving 1 male, the male landed with the female; in 3 of 9 two-male chases, 1 landed with the female, in 2 chases both landed with her, and in 4 neither male landed with the female; in 2 of 4 three-male chases 1 male landed with the female, and in 2 such chases none landed with her.[3] In terms of individual pursuit success, percentages are: 74% in one-male chases, 39% in two-male chases, and 17% in three-male chases. Table 1 gives information on some circumstances pertinent to unsuccessful pursuits. The following points seem significant: 8 (of the 28 total) unsuccessful pursuits occurred when the female turned off her light (Ia, IIIa1); and male-male interactions occurred in 12 (Ia1, IIa2, IIb1, IIIb1).

While the glow of a flying female is probably indispensible for eliciting male pursuit (signal function), it also is a beacon for male orientation during the chase. Pursued females eluded males by altering their light emission: 2 females landed and turned off their light; 2 others landed, turned off their light and then flew off without a light; and another began emitting a male-like flash. One series of observations is especially interesting: after copulating for at least 1 hr 35 min, then remaining alone on

[3]These data derived from natural and artificially induced chases.

the perch 5 min, a female flew off in low, hovering flight, glowing. A flashing male flew near, she extinguished her light and dropped to the ground. She then turned on her light and flew upward, the male resumed pursuit, she landed, turned off her light, moved to the other side of the leaf, and flew with her light off and without the male. Other females flew up into the trees or low over the ground and left pursuing males behind.

A number of interactions between males were observed. Many occurred in the presence of females. On 3 occasions males, that had been pursuing females that landed and stopped glowing, hovered over and landed beside flickering males that were perched nearby. They either separated immediately or did not interact further. In 5 two-male chases the males darted and orbited about each other (sparred) at or near the end of the chase.

TABLE 1: NOTES ON UNSUCCESSFUL PURSUITS

I. one-male chases (7 unsuccessful pursuits)
  a. female turned off her light (n = 5)
    1. male landed with perched, luminescing male (n = 2) (no data n = 3)
  b. male "lost" female, dropped out of chase (n = 2)

II. two-male chases (11 unsuccessful pursuits)
  a. other male landed with female (n = 3)
    1. male landed 18" away from female and successful male (n = 1)
    2. male sparred in flight with successful male, then flew off (n = 2)
  b. neither male landed with female (n = 8)
    1. males sparred and flew off together (n = 6, i.e. 3 prs.) two pairs of males landed together
    2. males dropped out of chase separately (n = 2)

III. three-male chases (10 unsuccessful pursuits)
  a. none (of the 3) landed with the female (n = 6, i.e. 2 trios)
    1. female turned off her light (n = 3)
    2. female eluded pursuers (n = 3)
  b. 2 of the 3 did not land with female (n = 4)
    1. males left chase and landed together (n = 2)
    2. males left chase when female and 3rd male landed together (n = 2) one male flew on, the other returned to his original perch

TABLE 2: NOTES ON SUCCESSFUL PURSUITS

I. one-male chases (20 successful pursuits)
  a. female flew off immediately, left male alone (n = 3)
  b. male mounted female immediately (n = 3)
  c. male and female began walking-luminescing interaction (n = 8)

II. two-male chases (7 successful pursuits)
  a. male landed with female alone (n = 3)
    1. female flew off immediately (n = 1)
    2. male and female began walking-luminescing interaction (n = 2)
  b. male landed with female and other pursuing male (n = 4, i.e. 2 pairs of males)
    1. male remained with female (n = 2)
      A. female flew off immediately (n = 1)
      B. male mounted female immediately (n = 1)
    2. male flew off, left other male with female (n = 2)

III. three-male chases (two successful pursuits)
  a. male landed with female alone (n = 2)
    1. male and female began walking-luminescing interaction (n = 1)
    2. female flew off immediately, male pursued her again, landed with her, male and female began walking-luminescing interaction as in IIIa1 (n = 1)

In 3 of these the males flew off together, still sparring, and left the female alone. In 2, one of the males landed with the female and the other male flew away.

In other instances of male interactions no females were present: males sometimes pursued flying males for a few feet, hovered near and darted toward perched luminescing males, and others landed beside perched luminescing males. I at first presumed one of the last-mentioned interactions to be a male-female interaction because of the luminescing pattern of the perched male.

Table 2 gives some details of successful pursuits (i.e. when a male pursued a female and landed with her at the end of the chase). In 6 instances the female flew off immediately after landing (Ia, IIa1, IIb1A, IIIa2). In only 1 of these did the male continue pursuit; in 3 the female flew off or dropped from her perch with her light off; and in 2 cases she flew with her light on, but the male did not follow. Figure 14 shows the sequences of continued male-female interactions observed to follow the landing of the 2 on a perch together. In 4 instances males mounted the females immediately (Table 2, Ib, IIb1B; Fig. 14, lower left; n = 4). One of the males was immediately knocked from the female by a raindrop and fell about 2 ft. He then flew back and landed about 1 inch from her. After a brief walking-luminescing interaction (see below) he flew off. In the 3 other cases in which the male immediately mounted the female, the interaction terminated after 1, 1.5 and 4 min. with the female flying away (10 inches, 18 inches, and up into the trees out of sight).

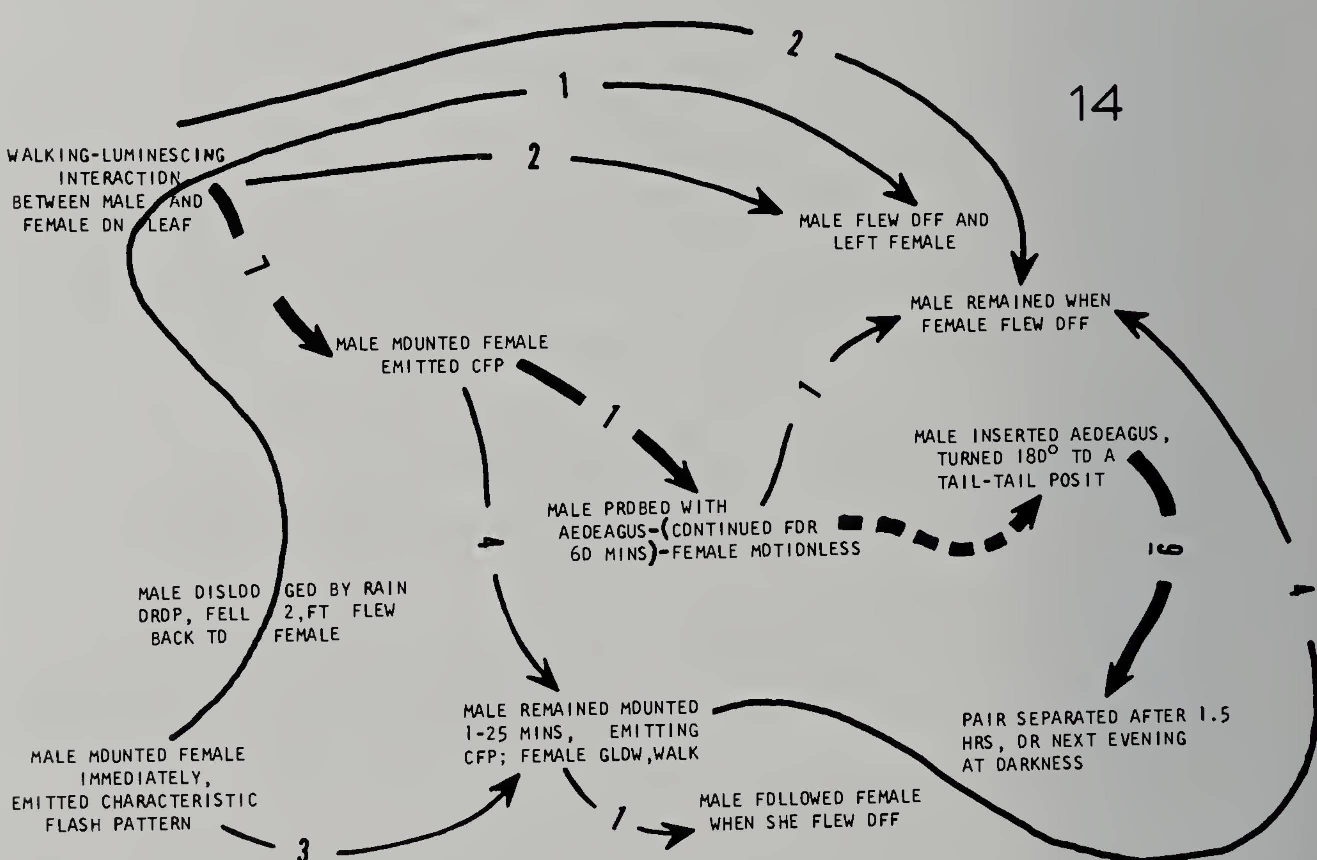

Fig. 14: Summary of behavior subsequent to chases (natural and artificial), after male and female landed together. Most pairs (n = 11) began walking-luminescing interaction (upper left). In 4 instances male mounted immediately (lower left). Heavy arrows suggest sequence in successful mating. Broken arrow indicates step not actually observed. Numbers indicate observations.

Walking-Luminescing Interaction

The next distinctive phase of mating behavior occurred after a male and female landed together at the end of the chase: it involved walking and luminescing (Fig. 14, upper left; n = 11). I observed 7 such interactions from beginning (landing) to end (mounting), and portions of 9 others. I discerned no lengthy stereotyped behavior sequences (reaction chains, Bastock, 1967) but noted a number of single elements common to some or all, and recurring combinations of 2 or 3 elements. In all interactions the predominant luminescent emission patterns of males were the same ones that predominated during the sedentary signalling phase—single flashes and flickers. In verbal notes (n = 52) on tapes made during observations, sequences of single flashes were noted 28 times; flickers, 8; rapid twinkles, 7; stepped flashes, 6; and beady glows, 3. The main emission patterns of females were glows (n = 20) and beady glows (n = 11), the ones that predominate in sedentary signalling. Other patterns were occulted glows (= glows with brief off periods) (n = 3), slow, dim pulses (n = 1), and glows with stepped modulations (n = 1).

Recurring locomotor elements were: male walks to female; female walks to male; male walks away from female; female walks away from male; male runs away from female; both motionless. The combinations of these elements noted were: male walks to female, male runs away quickly; female walks away from male, male walks immediately behind female; female walks to male, male walks to female; and female walks away from male, male walks away from female. Locomotor and luminescent elements were combined: female walks to male, male emits bright flicker; male walks to female, female glow intensity greatly increases; male emits bright pulses, female greatly increases glow intensity, female turns to face male; male and female motionless within 2 inches of each other, emit main luminescent patterns; male emits flicker and walks away from female; and female walks to male, male emits bright single pulses, male mounts female.

The following excerpts from descriptions of walking-luminescing interactions, modified from tape transcripts, better indicate the general nature of these interactions and give additional information about them: (1) pair on leaf 4 inches apart—female glows, male emits combination of bright pulses and flickers—male walks to female, then dashes away very quickly, she walks toward him and he emits a bright flicker—her glow intensity changes from time to time—female walks toward male, he toward her, they stop 0.5-0.75 inches apart—he flies off, she flies to ground; (2) pair on underside of leaf 0.75 inches apart—female glows, male emits rapid twinkles, then dims—male turns and faces female, female turns, walks away to 1.5 inches, stops—her body at right angles to his body axis—female glow occasionally broken with 2-sec dark periods (occulted) —male emits dim flashes, female emits beady glow, male twinkles rapidly, then emits bright crescendos, then rapid twinkles, dim single flashes—both remain motionless, body positions the same—female glow dims, then brightens, male twinkles rapidly then emits dim single flashes—female emits dim single flashes, then a dim glow, he emits bright single flashes, then rapid twinkles—he walks to her (1.5 inches), turns and runs away to 3 inches, then to 5 inches, her glow is occulted then beady . . . she emits dim glow, now beady, he emits stepped-flashes (Fig. 4)—he emits bright single flashes and walks to her, then a bright flicker, she flies away and he emits rapid twinkle, then stops . . .

Walking-luminescing interactions observed in their entirety lasted 1-4 min (n = 8), although one interaction, observed only in part, endured 40 min; they terminated with the male emitting a characteristic flash pattern consisting of very bright flashes at intervals of approximately 0.5 sec and mounting the female (n = 7), with the male flying away (n = 3), or with the female flying away (n = 2) (Fig. 13 and 14).

Mounting

The next distinctive stage of the male-female interaction was the mounting of the female by the male. In some cases this occurred immediately after the 2 had landed together (Table 2, Ib, IIb1B; Fig. 14), but more often it followed the walking-luminescing interaction described above. In either case it was always (n = 11) accompanied by a series of rhythmic, very bright flashes, the major component of each being 0.08-0.11 ($\bar{x}$ = 0.09, n = 43, 1 male) (Fig. 13) sec in duration and with a period of 0.67-0.72 ($\bar{x}$ = 0.71, n = 46, 1 male). In some instances males began this flash pattern a few seconds before mounting, but usually they began immediately before or while mounting. While males mounted and flashed, females were usually (9 of 11) motionless and did not luminesce, but since none of the mountings I observed progressed to copulation I do not know the behavior that is characteristic of successful courtship. Occasionally (2 of 11) females glowed and walked about during the entire time the male was mounted. One male remained mounted for 25 min and another for 60 min, although other pairs separated after 1.5-4 min. Some males, while mounted, flexed and extended (made probing motions with) the tips of their abdomens with genitalia extruded. At separation females appeared to take the active role. One male was able to briefly remount, but again the female left him. While mounted, males antennated the pronota of their females and grasped them with all legs: forelegs were positioned just anterior to the mid-elytra and the hind legs at the anterior edge of the elytral apical curves.

Copulation

Although none of the observed mountings led to copulation, several pairs were found already coupled. One pair was 2 inches above the ground on the undersurface of a blade of grass in a tail-to-tail position about 130 min after the beginning of chasing activity. The female glowed, nearly continuously, and the male emitted flickers and single flashes. They separated 95 min later. Then the male flew away immediately while the female remained on the perch emitting a beady glow for 5 min. When she flew, males perched nearby chased her and she eluded them. Other pairs were found during daylight and at dusk when flashing first began as noted above. One female apparently mated more than once; I marked her with paint at dusk when I found her a few inches from a male moments after he began flashing (see above), and I found her 24 hr later, again a few inches from a male that had just started flashing. One possible explanation for the absence of chases during the first 2 hr after sunset may be that during this time a high proportion of flying females have just completed copulating, and are flying about ovipositing before becoming receptive to males again.

Discussion

Pair formation in *L. obsoleta* is by far the most complex reported for any lampyrid. The fundamental stages seem to be (1) sedentary signalling, (2) chasing, (3) walking-luminescing, (4) mounting, and (5) copulating (Fig. 14, heavy arrows). The chase is perhaps comparable to signal system I found in other fireflies, except that in *L. obsoleta* the female is not a stationary broadcaster; the walking-luminescing interaction, and perhaps sedentary signalling, may involve system II.

The complexity of mating behavior suggests the possibility that *L. obsoleta* is actually a complex of cryptic species, and that the significance of the prolonged mating sequence is that it reduces mating mistakes among very close relatives since it maximizes opportunities (stages 1-4) for identification. It is difficult to understand the evolutionary maintenance of such an intricate and expensive mating system unless each element figures critically in something as indispensable as mating correctness. Ballantyne (1968), in her study of Australian and Indomalayan Luciolini, observed that *L. obsoleta* is morphologically variable in coloration. The 3 series that I collected, at Lae, Goroka, and Alexishafen, differ in coloration but each series is homogeneous. It is even possible, but I believe unlikely, that the study population at Alexishafen was actually composed of 2 (or more) species. Further study will perhaps disclose the presence of several species, and their study would, of course, provide important clues to the approach an experimental analysis of this mating system should take.

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